# Species-specific partitioning of soil water resources in an old-growth Douglas-fir–western hemlock forest

FREDERICK C. MEINZER,[1,2] JEFFREY M. WARREN[1] and J. RENÉE BROOKS[3]

[1] USDA Forest Service, Forestry Sciences Laboratory, 3200 SW Jefferson Way, Corvallis, OR 97331, USA

[2] Corresponding author (fmeinzer@fs.fed.us)

[3] Western Ecology Division, US EPA/NHEERL, 200 SW 35th St., Corvallis, OR 97333, USA

**Summary** Although tree- and stand-level estimates of forest water use are increasingly common, relatively little is known about partitioning of soil water resources among co-occurring tree species. We studied seasonal courses of soil water utilization in a 450-year-old *Pseudotsuga menziesii* (Mirb.) Franco––*Tsuga heterophylla* (Raf.) Sarg. forest in southwestern Washington State. Soil volumetric water content ($\theta$) was continuously monitored with frequency domain capacitance sensors installed at eight depths from 0.2 to 2 m at four locations in the vicinity of each species. Vertical profiles of root distribution and seasonal and daily courses of hydraulic redistribution (HR), sap flow and tree water status were also measured. Mean root area in the upper 60 cm of soil was significantly greater in the vicinity of *T. heterophylla* trees. However, seasonal water extraction on a root area basis was significantly greater near *P. menziesii* trees at all depths between 15 and 65 cm, leading to significantly lower water storage in the upper 65 cm of soil near *P. menziesii* trees at the end of the summer dry season. Greater apparent efficiency of *P. menziesii* roots at extracting soil water was attributable to a greater driving force for water uptake rather than to differences in root hydraulic properties between the species. The dependence of HR on $\theta$ was similar in soil near individuals of both species, but seasonal maximum rates of HR were greater in soil near *P. menziesii* because minimum values

co-occurring tree species. At the canopy level, eddy covariance techniques are providing increasingly detailed information about daily and seasonal courses of forest evapotranspiration (ET) and the key environmental variables that influence it (e.g., Berbigier et al. 1996, Irvine et al. 2004, Unsworth et al. 2004). Nevertheless, these techniques do not permit evaluation of the relative contributions of co-occurring species to daily and seasonal courses of ET unless compatible measurements are made at the individual tree and species scales. Sap flow techniques provide a means of estimating the contributions of individual species to canopy transpiration in mixed stands, provided the populations of trees sampled are representative of the composition of the stand as a whole (Sala et al. 2001, Bovard et al. 2005, Ewers et al. 2005, Fiora and Cescatti 2006). When used concurrently with eddy covariance measurements, continuous measurements of sap flow facilitate partitioning of canopy ET among individual species and soil and understory components over daily and seasonal timescales (Köstner et al. 1992, Loustau et al. 1996, Hutley et al. 2001). However, relating sap flow to the variables driving the daily dynamics of canopy transpiration is more complex because capacitance results in lags between changes in canopy transpiration and flow measured near the bases of the trees (Goldstein et al. 1998), especially in stands containing large

1999). Species-specific differences in vertical partitioning of soil water resources can be expected to result in considerable horizontal heterogeneity in vertical profiles of soil water storage, especially in seasonally dry environments.

Soil properties and processes often exhibit a high degree of spatial heterogeneity in natural forest stands, but the extent to which this is linked to heterogeneity in water utilization by vegetation is largely unknown. Certainly, soil physical properties can vary substantially over short vertical distances (Warren et al. 2005) and corresponding horizontal heterogeneity associated with variation in attributes such as parent material and deposition of organic matter occurs. Nevertheless, differences in soil water utilization among dominant species are likely to exert a strong influence on spatial variation in soil processes and competitive interactions among species. For example, both the root (Bryla et al. 1997, Irvine et al. 2005) and microbial (Falk et al. 2005, Tang et al. 2005) components of soil respiration diminish as the soil dries. In addition, localized differences in the timing and extent of soil water extraction are likely to affect the establishment and survival of understory species.

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) are among the most abundant and widely distributed coniferous species in western North America. They often co-occur in mixed stands, but their distributions extend to different extremes along a moisture gradient. Douglas-fir occurs in drier, interior sites, from which western hemlock is excluded, and western hemlock is found in wet coastal areas of British Columbia and southeast Alaska, where Douglas-fir is largely absent (USDA Forest Service 1990). Limited comparative data point to some physiological traits associated with the differences in abundance of the two species along an aridity gradient. Douglas-fir generally exhibits more negative minimum leaf water potentials than western hemlock (Bauerle et al. 1999, McDowell et al. 2002, Meinzer et al. 2004*a*) and its xylem is less vulnerable to embolism than that of western hemlock (Kavanagh and

penetrating to greater depths than those of western hemlock, depending on soil characteristics and depth of the water table (USDA Forest Service 1990). We hypothesized that the different ecophysiological characteristics of *P. menziesii* and *T. heterophylla* are reflected in different patterns of soil water utilization, leading to spatially distinct patterns of soil water extraction and storage in the vicinity of groups of trees of each species. We tested this hypothesis in a 450-year-old Douglas-fir–western hemlock forest by continuously monitoring vertical and horizontal variation in soil volumetric water content during consecutive seasonal dry periods between 2002 and 2005. Frequency domain capacitance probes with annular sensors allowed us to characterize detailed time courses of soil water extraction at eight depths, from 20 to 200 cm, at four locations in the vicinity of large individuals of each species for a total of eight locations. Measurements of the vertical distribution of roots near each species and of sap flow and leaf water potential in both species provided additional context for interpretation of spatial and temporal patterns of soil water extraction and storage.

## Materials and methods

### Site description

The study took place between 2002 and 2005 at the Wind River Canopy Crane Research Facility (WRCCRF), Wind River Experimental Forest, in southwest Washington State (371 m a.s.l.; 45°49′13.76″ N, 121°57′6.88″ W) where the mean annual precipitation is 2223 mm, of which ~119 mm falls during June through September, and mean annual temperature is 8.7 °C. Seasonal precipitation patterns during the study period are shown in Table 1. Measurements were carried out in a 4-ha plot of old-growth (450-year-old) Douglas-fir, western hemlock and western red cedar (*Thuja plicata* Donn) forest under the canopy crane. Stand density was 427 trees ha$^{-1}$, and basal area 82.9 m$^2$ ha$^{-1}$. Douglas-fir (35 trees ha$^{-1}$),

### Soil water content

Soil volumetric water content ($\theta$) was quantified with multi-sensor, frequency domain capacitance probes (Paltineanu and Starr 1997, Brooks et al. 2002, Warren et al. 2005). These probes contained eight annular capacitance sensors (Enviro-

installed between pairs of trees of the same species to minimize the influence of roots of other species. Distances from the probe to the closest tree of each pair ranged from 1 to 4.5 m for *P. menziesii* (mean = 2.75 m), and from 2 to 5 m for *T. heterophylla* (mean = 3.06 m). Mean DBH of the trees represented in Figure 1 was 1.10 ± 0.08 m for *P. menziesii* and 0.62 ± 0.07 m

The canopy crane and its suspended gondola provided access to the upper crowns of several large individuals of each species for measurements of leaf water potential ($\Psi_L$) with a pressure chamber (PMS Instrument Company, Corvallis, OR). Daily courses of $\Psi_L$ were measured during July and August on seven dates between 2002 and 2004. Typically, at each

upper 100 cm, root area was consistently lower near *P. menziesii* trees, but not significantly different from that near *T. heterophylla* trees at individual depths. However, mean root area in the upper 60 cm was significantly lower near *P. menziesii* trees ($P < 0.05$). Differences in root area accounted for about 86% of the variation in seasonal water extraction among

from the upper 15 to 35 cm of soil were similar near both species (Figure 4a). However, as $\theta$ approached 0.20 m³ m⁻³ rates of soil water extraction became greater near *P. menziesii* trees. Extrapolated values of $\theta$ at which soil water extraction would reach zero were 0.11 and 0.14 m³ m⁻³ for *P. menziesii* and *T. heterophylla*, respectively, for the data shown in Figure 4a. These values were consistently lower in the vicinity of *P. menziesii* trees during all years for which sufficient data were available (2003–2005, $P < 0.002$). It should be noted that
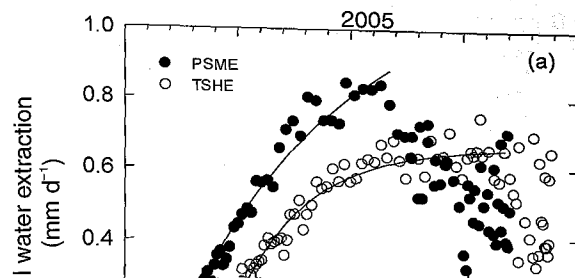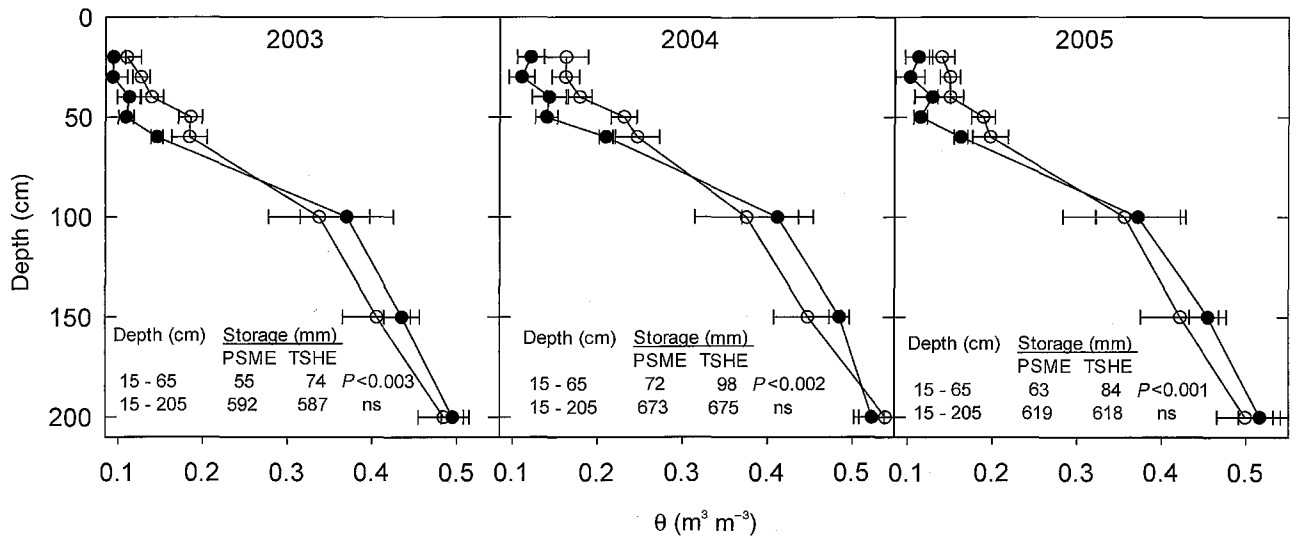
Figure 5. Vertical profiles of θ in the vicinity of *P. menziesii* (PSME) and *T. heterophylla* (TSHE) trees at the end of the summer drought period in three consecutive years. Horizontal bars represent standard errors ($n = 4$). In the lower portion of each panel, water content was integrated over the depth intervals shown, to obtain values of total soil water storage.
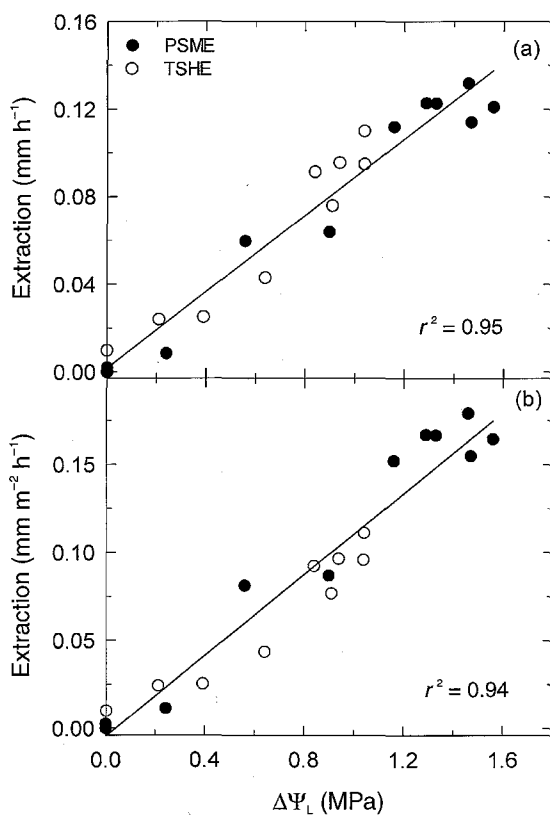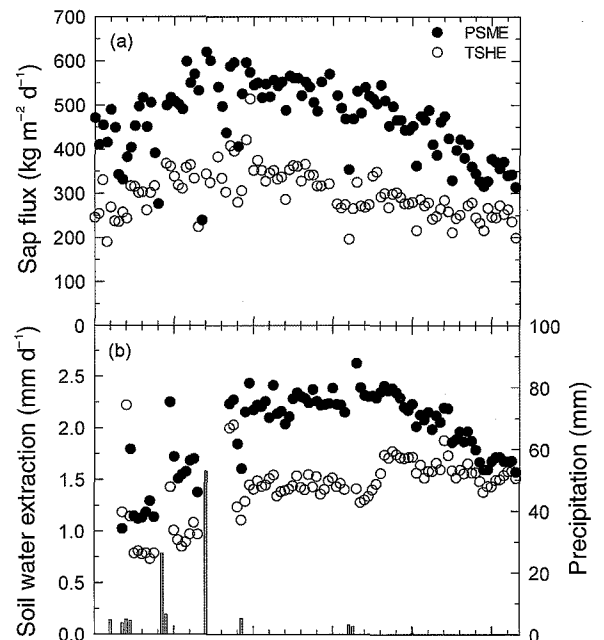


Figure 6. Rates of soil water extraction from the 15 to 65 cm layer near

of extraction tended to be greater near *P. menziesii* trees early in the season, with rates near both species converging by mid to late season (Figure 8). In 2003, measurements were not initiated until mid-season when rates of soil water extraction had apparently already converged. Daily courses of sap flow mea-
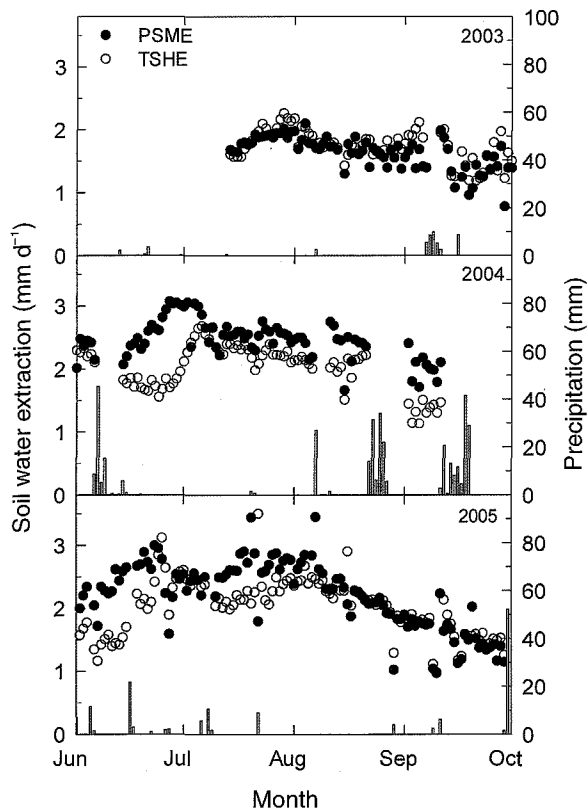
Figure 8. Seasonal courses of soil water extraction from the 15 to 205 cm layer in the vicinity of *P. menziesii* (PSME) and *T. heterophylla* (TSHE) trees. Precipitation events are indicated by vertical bars.
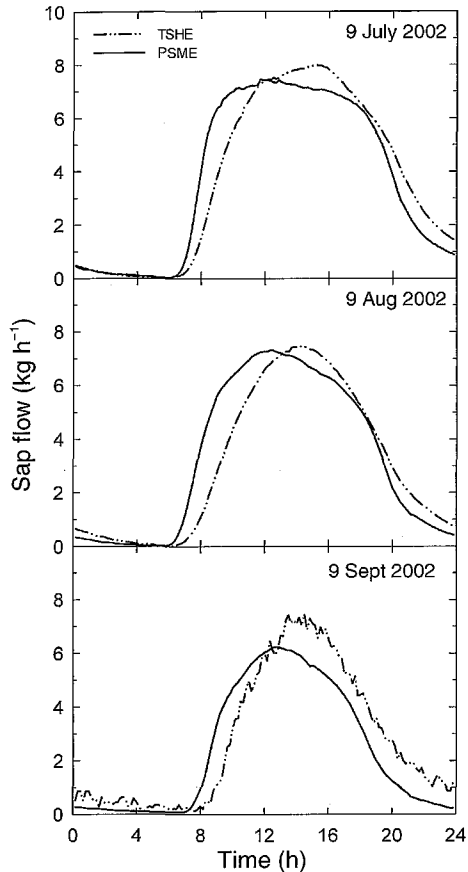


Figure 9. Representative daily courses of whole-tree sap flow during the summer of 2002. Data are means of three *P. menziesii* (PSME) and two *T. heterophylla* (TSHE) trees.

sured under clear dry conditions during the summer of 2002 showed that flow consistently began earlier and rose more sharply in *P. menziesii* (Figure 9). Consequently, maximum rates of sap flow were attained 1 to 4 h earlier in *P. menziesii* than in *T. heterophylla*, depending on the time of year. On July 9, sap flow remained at or above 90% of its maximum value for about 8 h in *P. menziesii* and only 5.5 h in *T. heterophylla*. On August 9, the duration of near maximal sap flow had diminished to 4.5 h in both species. On September 9, the duration of near maximal sap flow had shortened to about 4 h in *P. menziesii* and 3 h in *T. heterophylla*.

**Discussion**

that patterns of soil water utilization were closely associated with the proximity of large individuals of Douglas-fir versus western hemlock. Furthermore, measurements of whole-tree sap flow and water status provided independent confirmation of species-specific differences in relevant water relations traits.

*Root distribution and properties*

Despite significantly lower root area in the upper 60 cm of soil near Douglas-fir trees compared with western hemlock trees (Figure 2a), seasonal water extraction on a root area basis was consistently greater in Douglas-fir over this range of depth (Figure 3). Two principal mechanisms seem likely to have

draulic conductance was not measured directly, but similar relationships in the two species between $\Delta\Psi_L$ and rates of soil water extraction on a root area basis (Figure 6b), and between $\theta$ and hydraulic redistribution on a root area basis (Figure 4b) imply that their root hydraulic properties were similar.

In both species, increasing investment in root area between 100 and 20 cm depth (Figure 2a) yielded diminishing returns in terms of seasonal water extraction (Figure 2b). However, because nutrient availability is typically greater near the soil surface than at depth, the marginal gain in nutrient uptake per increment of root area may have been greater than that of water extraction. The exponential increase in root area between 100 and 20 cm was largely attributable to the increasing abundance of fine roots (Warren et al. 2005). The role of fine roots in meeting transpirational demands is usually emphasized because of their greater abundance (Warren et al. 2005) and permeability to entry of water than coarser suberized roots that penetrate to greater depths (Lindenmair et al. 2004). Nevertheless, rates of water extraction from the upper 205 cm remained relatively stable or even increased between June and August (Figures 7 and 8), whereas the relative contribution of roots in the upper 50 cm fell from about 50% in June to about 20% by the end of August (data not shown), implying that increased water uptake by deeper coarse roots, and possibly fine roots associated with them, compensated for diminishing water extraction by shallow roots (Bréda et al. 1995, van Rees and Comerford 1990, Lindenmair et al. 2004). Although Douglas-fir is reputed to develop a deeper root system than western hemlock, mean rates of water extraction between 100 and 200 cm depth were similar at 0.082 mm day$^{-1}$ for Douglas-fir and 0.079 mm day$^{-1}$ for western hemlock during the nearly rainless month of August 2005.

*Spatial patterns of soil water storage*

Consistently lower seasonal minimum values of $\theta$ in the upper 65 cm of soil near Douglas-fir trees (Figure 5) appear to have been a consequence of greater maximum driving forces for root water uptake in Douglas-fir than in western hemlock (Figure 6). The spatial patterns of seasonal minimum $\theta$ and water storage in the upper 65 cm of the soil profile observed in this study have a number of implications for plant, soil and successional processes. In the context of plant functioning, soil $\Psi$ is a more relevant and robust indicator than $\theta$ of the physiological availability of soil water. Therefore, water release curves previously determined for soils at the study site (Warren et al. 2005) were used to estimate seasonal minimum values of soil $\Psi$. In 2005, a year with a long rainless period during the summer, the lowest values of soil $\Psi$ were observed at the 20 and 30 cm depths, and ranged from a mean of −0.43 MPa at locations near Douglas-fir to −0.02 MPa at locations near western hemlock. Based on xylem vulnerability curves determined earlier for Douglas-fir roots at the study site (Domec et al. 2004), the minimum values of soil $\Psi$ observed were sufficient to provoke about 20% loss of root hydraulic conductivity due to embolism. However, in a nearby 24-year-old stand consisting almost exclusively of Douglas-fir, soil $\Psi$

fell to −1.2 MPa (Brooks et al. 2006) and roots experienced 50% loss of hydraulic conductivity during the dry season of 2002 (Domec et al. 2004). Xylem vulnerability curves were not determined for western hemlock, but based on their relative vulnerability to xylem cavitation (Kavanagh and Zaerr 1997, Sperry and Ikeda 1997), roots of western hemlock would likely exhibit greater seasonal loss of conductivity than those of Douglas-fir in shallow soil layers dominated by Douglas-fir roots. However, because soil $\Psi$ did not decline below −0.02 MPa near western hemlock trees, their roots were probably unaffected by embolism during these years at these locations.

Our results further imply that, at the more arid extremes of its range, the ability of Douglas-fir to operate at more negative minimum leaf water potentials would enable it to reduce soil $\Psi$ in the upper portion of the profile to a point at which western hemlock roots would no longer be able to extract water, thereby potentially preventing the establishment and survival of western hemlock seedlings. In the vicinity of Douglas-fir trees (Figure 4b), higher rates of HR delayed soil drying, but did not stabilize $\theta$ at a constant minimum value. Previous work in other ecosystems dominated by woody species suggests that HR does not stabilize $\theta$ until soil $\Psi$ falls below about −1 MPa (Meinzer et al. 2004b). The localized distribution and abundance of shallow-rooted understory species that are less efficient than Douglas-fir in extracting soil water may also be influenced by spatial patterns of water storage in the upper soil profile similar to those observed in our study site. In contrast, at the wetter extremes of Douglas-fir's range, where this species co-occurs with western hemlock, the greater shade tolerance of western hemlock would eventually enable it to replace Douglas-fir in the absence of severe disturbances such as stand-clearing fires.

The differences in water availability in the upper portion of the soil profile associated with the proximity of Douglas-fir trees versus western hemlock trees are likely to contribute to spatial variability in rates of soil $CO_2$ efflux, decomposition and nutrient release at our study site, particularly late in the dry season. Although horizontal and vertical heterogeneity in the distribution of roots and soil organic matter are undoubtedly significant determinants of the pronounced spatial variability of soil $CO_2$ efflux often observed in forests (Rayment and Jarvis 2000), a number of studies have documented a strong effect of soil water on soil respiration (Falk et al. 2005, Tang et al. 2005). Soil water deficits have been shown to reduce both the autotrophic (Bryla et al. 1997, Irvine et al. 2005) and heterotrophic (Tang et al. 2005) components of soil respiration.

*Temporal patterns of water use*

Douglas-fir and western hemlock exhibited different patterns of water utilization at both daily and seasonal time scales. Throughout the summer, sap flow consistently increased more rapidly in the morning and attained maximum values earlier in the day in Douglas-fir than in western hemlock trees (Figure 9). Because capacitance results in time lags between

changes in transpiration and changes in flow at the base of the tree (Goldstein et al. 1998), differences in the daily course of crown transpiration were probably more pronounced than suggested by the sap flow data. Earlier studies conducted at the site have shown that capacitance in the size class of trees studied here is substantial in both species, but greater in Douglas-fir (Phillips et al. 2003, Meinzer et al. 2006). Although differences in daily courses of sap flow are often related to crown height (Martin et al. 1997, 2001), the heights of the trees in which sap flow was measured were similar (52–58 m). The patterns seen in Figure 9 are likely to be accentuated in trees representing the mean height of each species in the stand, which was 52 m in Douglas-fir and only 19 m in western hemlock. The large difference in mean height would result in Douglas-fir crowns being illuminated earlier in the day and receiving high irradiances over a greater portion of the day.

At the seasonal time scale, total daily soil water extraction was typically greater near Douglas-fir trees than near western hemlock trees in the late spring and early summer, but rates of water extraction had largely converged by July to September depending on the year (Figures 7 and 8). The similarity in the seasonal patterns of sap flux and soil water extraction data collected concurrently during 2002, strongly suggests that the spatial and temporal patterns of soil water extraction characterized with the frequency domain capacitance probes were determined largely by the trees nearest to the locations where the probes were installed (Figure 1). Moore et al. (2004) working in a 450-year-old Douglas-fir–western hemlock forest in western Oregon also found that total daily sap flux was greater in Douglas-fir throughout much of the growing season, but that sap flux steadily converged and became nearly identical in the two species by September. These seasonal patterns imply that because rates of water utilization are intrinsically higher in Douglas-fir (Meinzer et al. 2005), its upper roots could experience limiting soil water deficits earlier in the dry season than those of western hemlock. Although roots of both species are able to tap more abundant water at depth, Warren et al. (2005), working at our study site, found that water extraction from the upper 2 m of soil decreased in a linear fashion as soil $\Psi$ at 20 cm declined, suggesting that the physiological status of shallow roots influences stomatal regulation of canopy transpiration independently of the status of deep roots (Domec et al. 2004, 2006).

## Acknowledgments

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